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Amber Fossil Scatopsidae (Diptera: Psychodomorpha). I. Considerations on Described Taxa, *Procolobostema roseni*, new species, from Dominican Amber, and the Position of *Procolobostema* in the Family

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ABSTRACT

The fossil Scatopsidae are reviewed. For Meunier's species in Eocene Baltic amber: *Scatopse fasciola* Meunier is transferred to *Ectaetia*; *Scatopse subsimilis* Meunier is transferred to *Rhegmoclemina*; and *Scatopse grassaris* Meunier and *Scatopse crassicornis* Meunier are considered unplaced in the Scatopsidae. *Protoscatopse jurassica* Rohdendorf and *Mesoscatopse rohden-dorfi* Kovalev are kept as Scatopsoidea incertae sedis. The generic placement of *Reichertella fasciata* Melander is retained. *Scatopse bilaminata* Cook and *S. primula* Cook from Upper Miocene/Lower Oligocene Chiapas amber are removed to Rhegmoclematini incertae sedis. *Procolobostema* is accepted as a valid genus. *Procolobostema*

longicorne Cook is synonymized with *P. hurdi* Cook. *Procolobostema incisum* Cook and *P. obscurum* are also indicated as possible junior synonyms of *P. hurdi* Cook. A new species of the genus *Procolobostema* Cook is described based on large series of males and females in Dominican Republic amber (early Miocene). The differences between the Chiapas and the Dominican Republic species of the genus are considered. The phylogenetic position of the genus in the Scatopsidae is discussed. *Procolobostema* certainly belongs to the Colobostematini. *Borneoscatopse* Freeman, known from a single Recent species described from one male from the Oriental Region, is considered the sister group of

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Procolobostema. This corresponds to an Oriental Region/Caribbean biogeographical component, similar to that seen in *Valesegya* (Anisopodidae). This may correspond to a more general pattern of distribution, which could be related to the

geological evolution of a fragmented Pacifica continent. Because Mexico and Hispaniola were already separated at the Miocene, independent extinction would have to be admitted for these species of *Procolobostema*.

INTRODUCTION

The Scatopsidae are a small and rather poorly known group of dipterans. Not more than 350 Recent species have been described to date, but at least 120 undescribed species are already known for the Neotropical region. Although not particularly large in terms of described species, the Scatopsidae probably have an old and venerable history. There are nearly 30 monophyletic subgroups in the family that show intercontinental relationships and that may have been differentiated in Pangaean times (Amorim, 1982b).

Knowledge of fossil Scatopsidae is limited: only 13 fossil species have been formally described. Fossil scatopsid literature is restricted to the papers of de Serres (1829), Loew (1850), Meunier (1907), Rohdendorf (1938, 1946, 1974, 1991), Melander (1949), McAlpine and Martin (1969), Cook (1971, 1981, 1990), Zherichin and Sukacheva (1973), Saigusa (1974), Keilbach (1982), Kalugina and Kovalev (1985), Kovalev (1986), Schumann and Wendt (1989), and Ross and Jarzembowski (1993) (see catalog of fossil Diptera, by Evenhuis, 1994). Important additional Cretaceous and Tertiary fossil specimens are now available and the paleontological study of scatopsids seems particularly timely. An appropriate analysis of the paleontological information of the family together with knowledge of the Recent species would allow important conclusions on the systematics and evolution of the Scatopsidae. This line of investigation might also supply interesting clues on general history of evolution and extinction from the Jurassic to the Recent. Before the new fossil species are described, however, remarks should be made on the state-of-the-art of the scatopsid fossils.

ACKNOWLEDGMENTS

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DESCRIBED FOSSIL SCATOPSIDAE

The first fossil attributed to *Scatopse* (later to become the type genus of the family) was referred by de Serres (1829), to the Tertiary of Aix-en-Provence, southern France. The absence of illustrations, however, makes a generic or even a subfamilial placement of the species impossible from the brief description given ("une espèce à corps et à ailes brunes"). However, one would not expect better taxonomic treatment from a fossil specimen than the one given by de Serres because scatopsid systematics was embryonic at that time. Loew (1850) referred to "*Scatopse*" specimens in amber without a formal description. Much later, Keilbach (1982) named one of the specimens discussed by Loew (1850).

Meunier (1907) formally described the first four scatopsid fossil species from Baltic amber. From these, "*Scatopse*" *fasciola* Meunier would have 9 or 10 flagellomeres and "*Scatopse*" *crassicornis* Meunier 10 flagellomeres, so they cannot be assigned to the Aspistinae, Psectrosciariinae, Scatopsini, Colobostematini, Swammerdamellini, or to *Rhegmoclemina*, in the Rhegmoclematini. Consequently, they could belong to the Ectaeiinae or to some other Rhegmoclematini genera. The drawing of the wing of "*S.*" *fasciola*, with a basal fusion of M_1 to R_s , strongly suggests that it may belong to *Ectaeitia* and the species is herein transferred to the genus. Very little can be said of "*S.*" *crassicornis*.

Meunier (1907: 395) commented that the "distance between the first and second longitudinal veins at the wing edge is greater than that which is usually the case in *Scatopse grassaris*" of the male of his series. However, the wing of *S. grassaris* is not pictured in Meunier's (1907) paper. It could be another species of *Ectaetia*, but no positive generic placement can be given for this species without examining the type specimens. For the time being *S. crassicornis* is kept as Scatopsidae incertae sedis.

The antennae of "*S.*" *grassaris* and "*S.*" *subsimilis* have eight flagellomeres; therefore, they could fit into the Aspistinae, Psectrosciarinae, Scatopsini, Colobostematini, Swammerdamellini, or in *Rhegmoclemina*, in the Rhegmoclematini. Meunier (1907: 393) described for "*S. grassaris*" a rather large distance between the "small cross-vein (at the base of the second longitudinal vein) and the edge of the wing." This statement is hard to interpret. It might indicate that the wing has relatively large r_1 and r_5 cells. *Scatopse grassaris* should also be referred to as Scatopsidae incertae sedis until the types are re-examined. The shape of the medial fork and the sigmoid shape of CuA_2 , on the other hand, indicate that *S. subsimilis* certainly belongs to the Rhegmoclematini. The existence of only eight flagellomeres is a reliable indication that it belongs to *Rhegmoclemina* and the species is herein transferred to that genus.

Rohdendorf (1938) described a fossil from the Upper Jurassic of Kazakhstan, *Protoscatopse jurassica*, for which he created the family Protoscatopsidae (Rohdendorf, 1946; see also 1974, 1991). His drawing of the wing of this species is similar to that for Recent Scatopsidae except for two "veins" forking from R_5 . M_1 is interrupted and only one of the cubital veins is depicted. It is well known that Rohdendorf depicted some of the cracks and artifacts on compression fossils as veins (Hennig, 1981). Kovalev (in Kalugina and Kovalev, 1985) stated, after reexamination of the holotype and additional undescribed material from Karatau, that one vein actually branches from R_s (that would be R_4), other "overnumbered" radial cross-veins probably being artifacts. This indicates that *P. jurassica* could indeed share the ple-

siomorphic condition of a feature synapomorphic for Scatopsidae; therefore, it would be excluded from the family. The basal interruption of M_1 is observed in different groups of Scatopsidae—as in the Aspistinae, Psectrosciarinae, and some Rhegmoclematini genera (*Rhegmoclema*, *Thripomorpha*, and *Parmaferia*) (see Haenni, 1994 for the synonymy between *Thripomorpha* and *Aldrovandiella*, which is accepted in Amorim [1994] as a separate genus), but is also present outside the family. It seems best at this time to leave *Protoscatopse jurassica* unplaced within the Scatopsoidea until more information becomes available.

Melander (1949) described a compression fossil from Miocene deposits in Florissant, Colorado, *Reichertella fasciata*. Many species of other insect families in the Florissant deposits are very finely preserved, but none of the posterior wing veins are preserved in the type of *Reichertella fasciata*. Some features, however, support Melander's (1949) generic classification of the fossil species (even considering that the concept of *Reichertella* changed considerably since his times). The short antenna, short palpus, large size of the abdominal sclerites, and the extension of R_5 (features presented by the fossil specimen) are shared by the Scatopsini sensu stricto, which includes only *Scatopse*, *Apiloscatopse*, *Reichertella*, and *Pharsoreichertella*. The long vein R_5 in fact is a plesiomorphic feature, but the other genera of Scatopsini do not present an R_5 quite closely parallel to C along most of its length. *Apiloscatopse* and *Pharsoreichertella* have R_5 gradually approaching C, while *Scatopse* has it parallel, but quite apart from C. Hence, there seems to be no good reason to propose a change of the generic placement of *Reichertella fasciata*, except if additional information becomes available.

Cook (1971) described seven Late Oligocene/Early Miocene fossil species of Scatopsidae based on 10 amber specimens from Chiapas, Mexico. Two of these species were assigned to *Scatopse*, one to *Swammerdamella*, and four to *Procolobostema*, a genus created for those species. *Scatopse bilaminata* and *S. primula* present obvious features of the Rhegmoclematini, particularly the sigmoid shape of CuA_2 and a mesal constriction

of the medial fork. *S. bilaminata*, according to the original description, would present "nine-segmented" antennae, whereas *S. primula* would have "twelve-segmented" antennae. A 10-segmented flagellomere would indicate that *S. primula* belonged to *Neorhegmoclemina* or to *Parascatopse*. Indeed, the female terminalia drawing made by Cook (1971: fig. 4) closely resembles the female terminalia of the Recent species of these genera, but it is not possible now to decide to which genus it should be assigned. A seven-segmented flagellomere, on the other hand, is known only in *Austroclemina* within the Rhegmoclematini. Also, the male terminalia drawings presented by Cook (1971: figs. 1–2) for *S. bilaminata* differ from any Recent group of the tribe. The wing venation is a strong indication that it belongs to the Rhegmoclematini but it is not possible to find a better placement for the species without examining the type. For the time being, it would be advisable to maintain *S. bilaminata* and *S. primula* as Rhegmoclematini incertae sedis.

There seems to be no doubt that the generic placement proposed by Cook (1971) for *Swammerdamella prima* is correct, according to the description, even though the wing of the partially destroyed type is not illustrated. The examination of the types of Cook's (1971) fossil species of *Swammerdamella* and *Neorhegmoclemina* would help to determine their relationships to the Recent fauna of the family (specimens were still unavailable for study from the Museum of Paleontology, University of California, Berkeley). *Procolobostema*, as discussed below, is accepted as a valid genus. Study of a large series of *Procolobostema* in Dominican Republic amber, however, suggests that Cook's (1971) taxonomy of that genus should be reconsidered.

First, the holotype of *P. hurdi* is certainly a female, not a male, as the examination of *P. roseni*, new species, makes clear. Second, the differences referred to by Cook (1971) between *P. hurdi* and *P. longicorne* are restricted to the length of body setae. Differences in setae length on amber specimens, however, may be an artifact, caused by a number of factors (air layers over the sclerites, compression of the matrix, inclination of

the setae, etc.). Moreover, the terminalia of the holotype of *P. longicorne* are said to be obscured by an air bubble; other features, including venation and the seventh abdominal segment, are "much like" those of *P. hurdi* (Cook, 1971). These are all indications that *P. longicorne* should be a junior synonym of *P. hurdi* (this latter name promoted because of page precedence).

The stronger alleged difference between *P. incisum* and *P. hurdi*, on the other hand, is the shape of vein M_1 . In *P. hurdi*, M_1 would have an angle at the position where the spurious vein r-m normally lies, with a fold at that point. The examination of a large series of *P. roseni*, n. sp., in Dominican amber shows that the shape of this vein is subject to intraspecific variation, females having a more defined angle, frequently with a spur. Consequently, this alone should not be a criterion to distinguish between species. The drawing (Cook, 1971: fig. 10) of tergite 7 of *P. incisum* shows a rather deep posterior incision, which also appears—although not so deep—on tergite 7 of *P. roseni*, n. sp. The drawing of the terminalia of *P. hurdi* does not exhibit any posterior incision, which suggests that *P. incisum*—if it is in fact a female—indeed corresponds to a species separated from *P. hurdi*. If the drawing of *P. hurdi* (Cook, 1971: fig. 8), on the other hand, is imprecise and the incision is present or if the specimen is a male (which is doubtful), both species may be conspecific. Since Cook (1971) apparently failed to discern between males and females in his material, it is quite difficult to determine whether *P. incisum* should be compared to males or females.

Lastly, the holotype of *P. obscurum* was described as "male(?)." The drawing of the male terminalia does not allow a detailed understanding of the terminalia sclerite morphology, but it is most certainly a male specimen. Tergite 7 of *P. obscurum* is clearly different from that of *P. roseni*, n. sp. Cook (1971) probably did not consider *P. obscurum* conspecific with *P. hurdi* because he accepted the type of *P. hurdi* as a male. Since the type of *P. hurdi* is almost certainly a female, there are rather strong indications that they could be the same species. However, synonymization should wait for examination of the types. Cook (1971) studied a small

series of *Procolobostema* specimens, which certainly made it difficult to assess intraspecific variation and perhaps even sexual differences. More definitive conclusions about the identity of Cook's (1971) species of *Procolobostema* should await the study of the types, which were unavailable for this study.

Kovalev (in Kalugina and Kovalev, 1985) described *Mesoscatopse rohdendorfi* from a Siberian compression fossil species from the Lower/Middle Jurassic, included in the family Protoscatopsidae. *M. rohdendorfi* shows a number of features that plausibly are absent from the stem group of the recent Scatopsidae, including a branched Rs. A discussion will be presented elsewhere to address the problem of this species. Kovalev placed the species in the family Protoscatopsidae, together with *Protoscatopse jurassica*, but indications of the monophyly of the taxon are still wanting. For now, the species should be included as incertae sedis in the Scatopsoidea.

Kovalev (1986) also described a Lower Cretaceous Mongolian scatopsid compression fossil with no wings preserved. Kovalev (1986) preferred not to describe it as a new species or give a familial placement to the fossil and he referred to it as "Scatopsoidea" "gen. sp." incertae sedis." There is, however, information that allows a more detailed discussion. Kovalev (1986: 141) referred to a flagellum with "7 or 8" flagellomeres. The shape of these flagellomeres (Kovalev, 1986: pl. XV, fig. 8), together with an illustration of the shape and the proportions of the thorax and abdomen, are sufficient not only to assign it to the Scatopsidae, but also to indicate that it may belong to the Scatopsinae, possibly fitting either in the Rhegmoclematini (in this case in *Rhegmoclemina*), Colobostematini, or Swammerdamellini.

Cook (1990) included a brief systematic discussion of a pair of male and female specimens in copula in a piece of Dominican amber belonging to *Neorhegmoclemina*. After examining a large series of probably conspecific specimens of the same deposit, I would agree that Cook's (1990) placement is correct. The species will be formally described later in this series of papers.

As stated above, important additional amber material is now available, particularly

from the Cretaceous of Canada, New Jersey, Lebanon, and Taymyr, as well as a considerably larger collection of more recent fossils from the Dominican Republic, Chiapas, and the Baltic. This is the first paper of a series describing this material, which also discusses the relationships of the fossil species with the recent fauna of Scatopsidae. Measurements are given in millimeters.

Procolobostema Cook

Procolobostema Cook, 1971: 60. Type-species, *Procolobostema hurdi* Cook, 1971 (= *Procolobostema longicorne* Cook, 1971, new synonym).

Procolobostema roseni, new species

(figs. 1-14)

MATERIAL EXAMINED: Holotype, male, **Dominican Republic**, specific locality unknown, AMNH, DR-10-956. Paratypes: same data, 1 male, AMNH no. DR-10-956 (with a specimen of *Neorhegmoclemina* and an antenna); 1 male, AMNH DR-10-945; 1 female, AMNH, DR-6-92; 1 female, AMNH DR-10-953; 1 female, AMNH DR-10-940; 1 male, AMNH DR-6-94; 2 males, 1 female, AMNH DR-8-177; 1 female, AMNH DR-10-948; 1 male, 2 females, AMNH DR-6-100; a male swarm, DR-SH-30; 1 male, El Valle, AMNH DR-6-43; 1 female, same, AMNH DR-6-40; 1 female, La Toca, AMNH DR-5-80; 1 female, and a part of a female, same data, but Santiago area, purchased from J. Brodzinsky, AMNH 11682; 1 male, same, but AMNH 11681; 1 female, AMNH 11794; 1 female, AMNH 11674; 1 female, AMNH 11675; 1 female, AMNH 11678; 1 female, AMNH 11685; 1 female, AMNH 11672; 1 male, AMNH 11679; 1 female, AMNH 11683; 2 males and part of a male, AMNH 11670; 1 male, AMNH 11673; 1 female, AMNH 11669; 1 male, AMNH 11680A; 1 female?, AMNH 11691C; 2 males, AMNH 11671; 1 female, AMNH 11801; 1 female, AMNH 11677; a large male and female swarm, AMNH DR-14-628 (together with two isopteran workers, a winged ant, a spider, and a drosophilid); 1 male, NHM Pal. PI II 386 (2); 1 male, NHM Pal. PI II 167 (together with a female of *Ectaetia*, to be described elsewhere); 1 male, "purchased

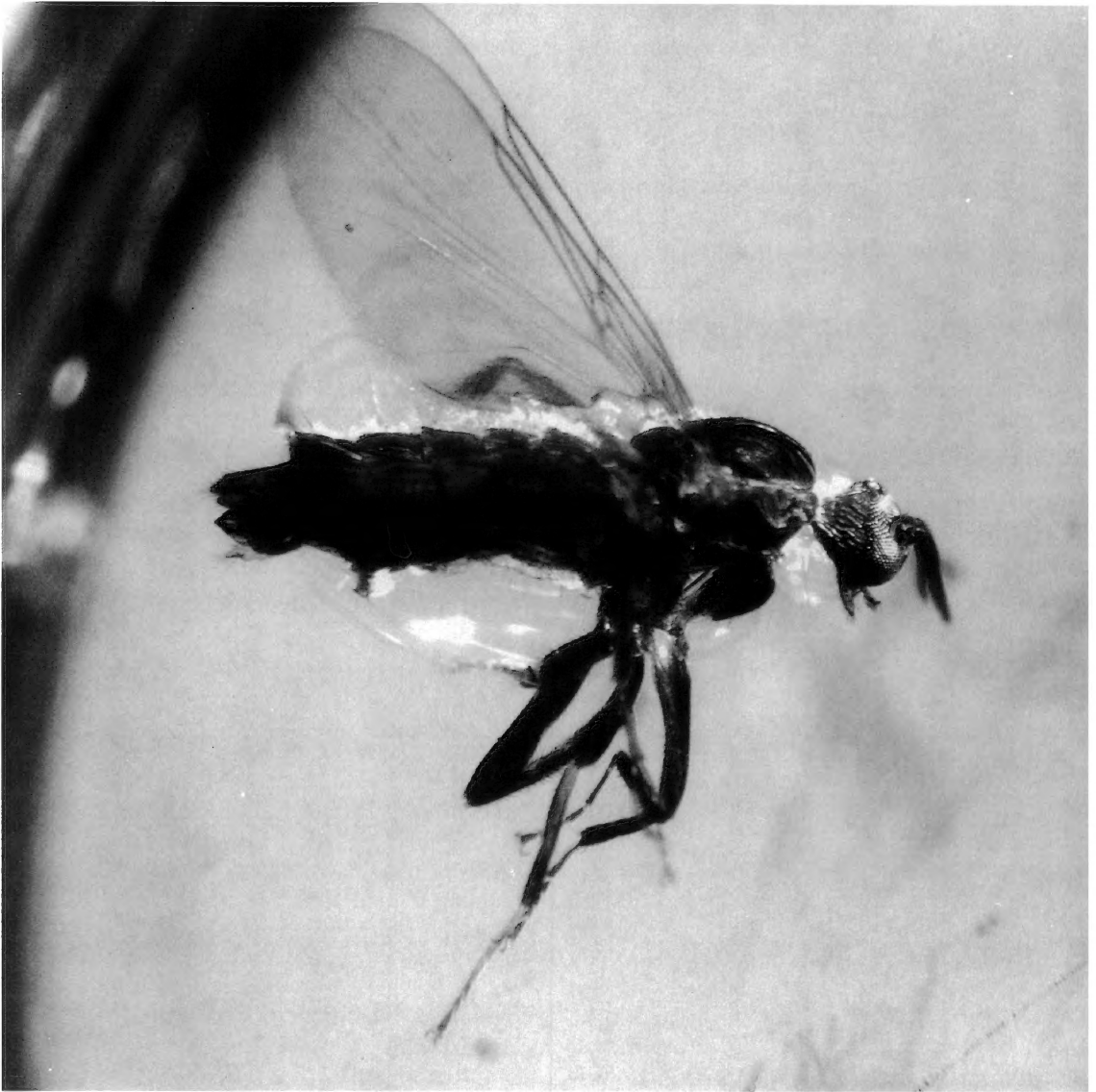


Fig. 1. *Procolobostema roseni*, n. sp. Male holotype, habitus.

McCallum, Marcus, 1993," NHM Pal. PI II 158; 1 male, same, NHM Pal. PI II 160; 1 male, NHM Pal. PI II 163; 1 male, NHM Pal. PI II 482 (1); 2 males, NHM Pal. PI II 157; 1 male and 1 female, NHM Pal. PI II 175; 2 females, NHM Pal. PI II 176; 3 females, NHM Pal. PI II 172; 1 female, NHM Pal. PI II 171; 1 female, NHM Pal. PI II 174; 1 female, NHM Pal. PI II 155; 1 female, NHM Pal. PI II 173; 1 female, NHM Pal. PI II 161; 1 female, NHM Pal. PI II 165; 1 female, NHM Pal. PI II 384 (2); 1 female, NHM Pal. PI II 156; 1 female, NHM Pal. PI II 169;

posterior half, female, NHM Pal. PI II 544 (2).

MALE: Total body length, 2.15–2.24 mm (\bar{x} = 2.20; N = 2). Habitus, fig. 1.

Head (figs. 3–5). Antenna brown, except for yellowish-brown pedicel and scape; with eight large flagellomeres, each with a single crown of setae, except the last and the first, each with two crowns; first flagellomere longer than remaining flagellomeres (figs. 3, 4). Occiput dark brown. Palpus yellowish, short, rounded, apically truncated by the sensory pit opening. Palpus length 0.10. Labella

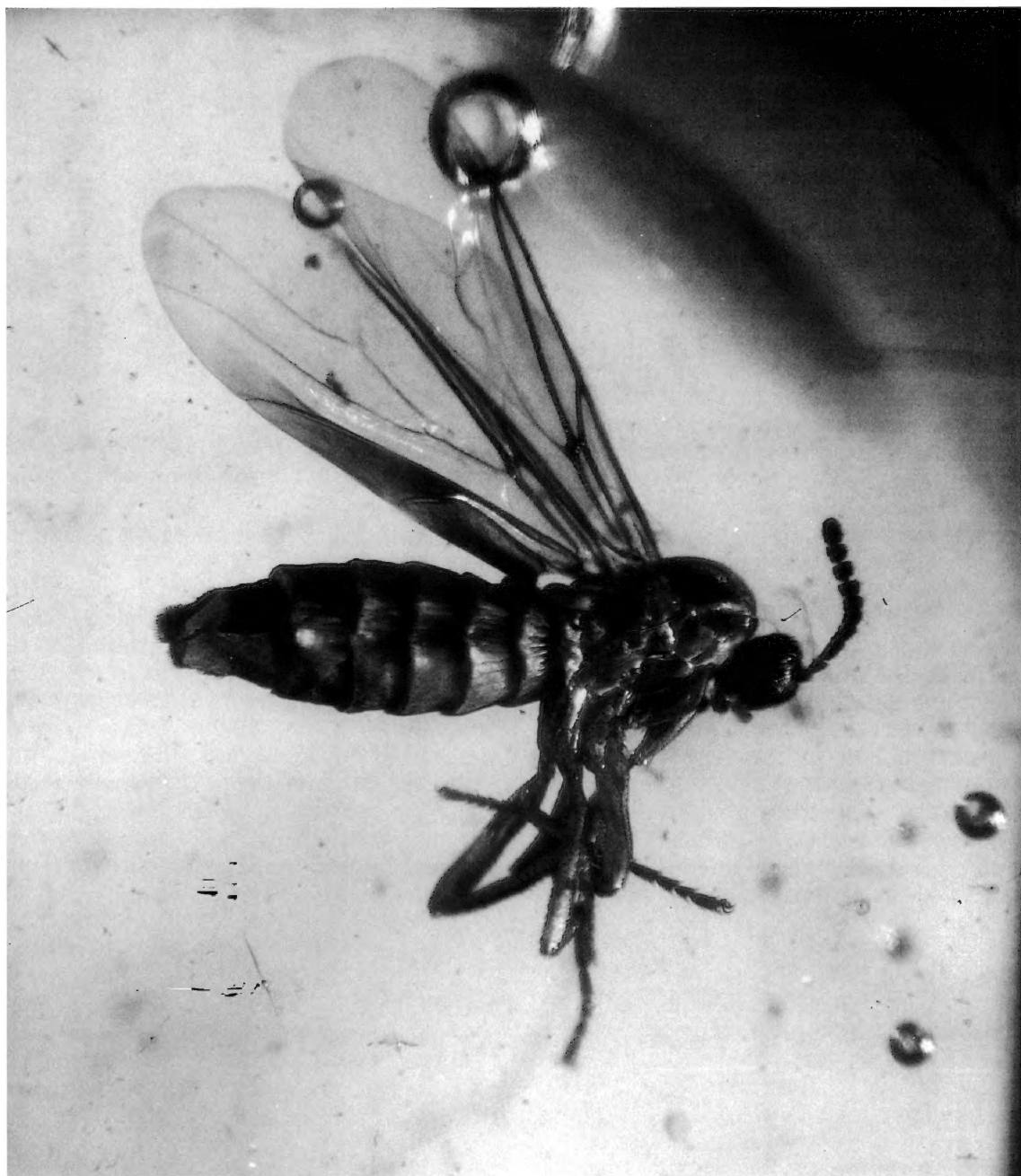


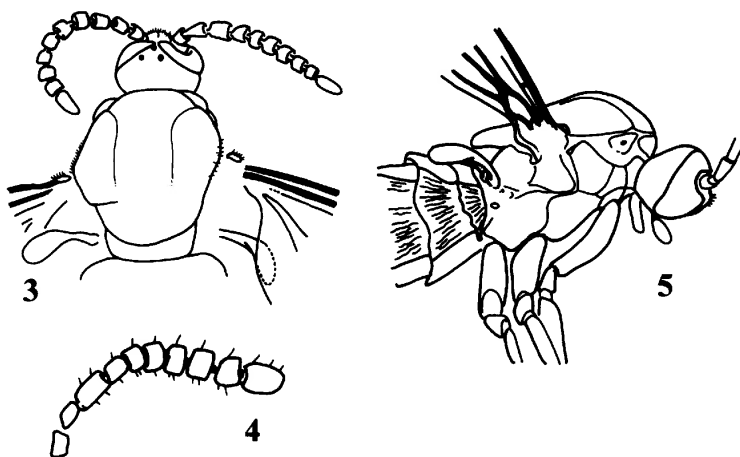
Fig. 2. *Procolobostema roseni*, n. sp. Female paratype, habitus.

short. Cardio-stipes apparently fused together mesally (fig. 5).

Thorax (figs. 3, 5). Mesonotum dark brown, with some slightly lighter longitudinal stripes, scutellum light brown with a transverse posterior, blackish-brown stripe. Scutum as long as wide, with a well-marked

transverse suture; 8–9 supra-alars. Pleural sclerites dark brown to dark orange-brown; spiracular sclerites (dorsal epimeron I) large, with spiracle quite large, in a mesal position. Suture between ventral epimeron I and anepisternum conspicuous.

Legs. Dark brown with light yellow tarsi.

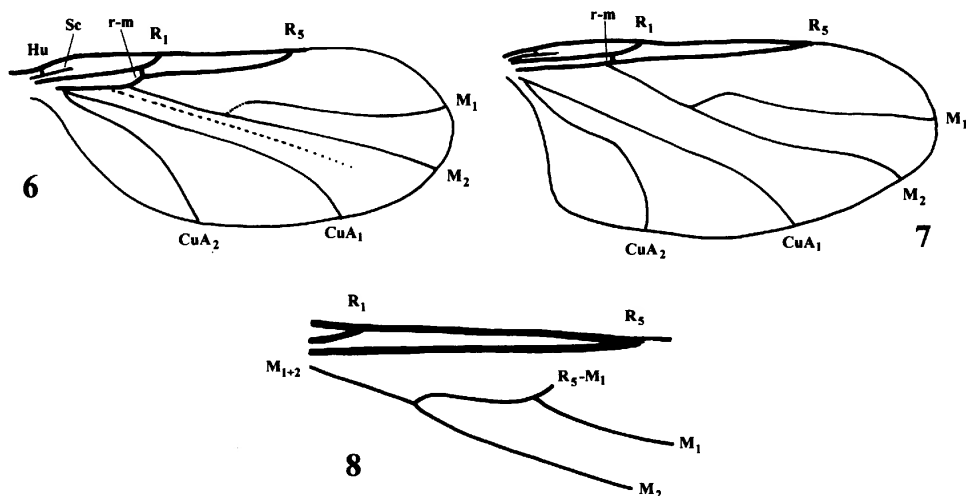


Figs. 3-5. *Procolobostema roseni*, n. sp. 3. Female paratype, dorsal view of head and thorax. 4. Same, antenna. 5. Same, lateral view of head, thorax, and base of abdomen.

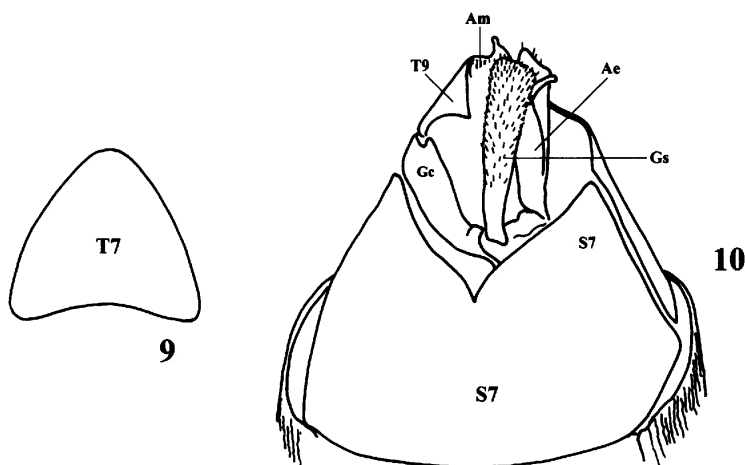
Wing (figs. 6-8). Total length 1.85-1.96 mm (\bar{x} = 1.91; N = 2). C1 (base of the wing to end of R_1) = 0.95; C2 (end of R_1 to end of R_5) = 0.95. Sc extending beyond Hu, but quite short and faint; R_5 long, ending in C well beyond M fork, but cell r5 slender. M_1 usually with a slight basal angle, spurious r-m vein absent in most males. True r-m very short, but present (no fusion of base of M_{1+2} to R_5). A node of sclerotization at the base of the CuA fork. CuA₁ curved posteriorly near apex; CuA₂ with two posterior curves, the first on distal $\frac{3}{5}$, the second near margin. No macrotrichia on posterior veins or on the

wing membrane, but membrane ochre-yellow.

Abdomen. Sclerites light brown, with lighter pleural membrane. On each segment (especially segments 4-6), pleural membranes more developed posteriorly than sclerites, so segments partially overlap. Tergite 7 (fig. 9) and sternite 7 very close together, but not fused into a ring around the terminalia. Terminalia as in figure 10. Gonocoxites modified into a slender lateral band fused to each other dorsally; gonostyle long with apex wider than base, setose for entire length; aedeagus elongated, with tubular



Figs. 6-8. *Procolobostema roseni*, n. sp. 6. Male paratype, wing. 7. Female paratype, wing. 8. Female paratype, detail of wing.



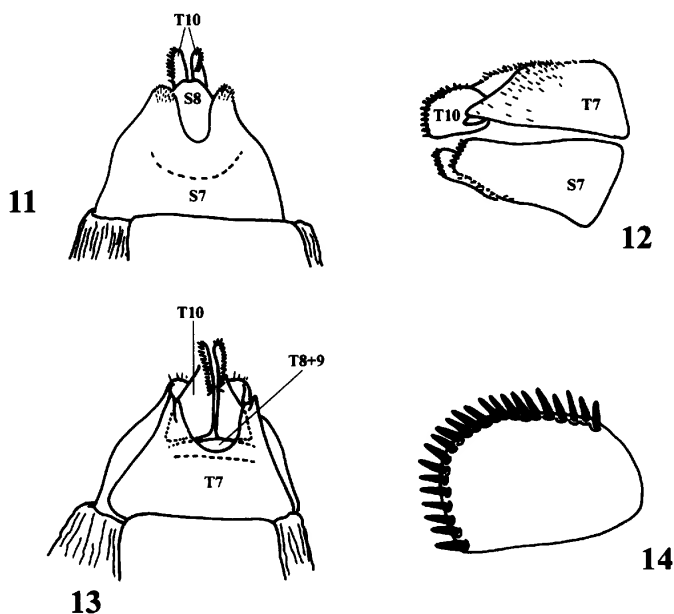
Figs. 9, 10. *Procolobostema roseni*, n. sp. 9. Male tergite VII. 10. Male sternite VII and terminalia. Gc gonocoxite; Gs gonostyle; T9 tergite 9; Am anal membrane.

apex curved ventrally; parameres absent; T9 well sclerotized.

FEMALE: Total body length, 2.77–3.00 (\bar{x} = 2.89, N = 2), considerably larger than males. Palpus length, 0.12. Habitus, figure 2. Wing length, 2.70. Considerably larger than the males; the scutum is usually wider. Wing differs from those of males especially on M_1 , more commonly with an angle or a short spur, and R_5 slightly more separated from C.

Tergite and sternite 7 considerably developed, both with mesal posterior incisions. Terminalia as in figures 11–13. Tergite 8 + 9 slender, rectangular, apparently bare; lobes of tergite 10 with typical spinose setae on distal border.

ETYMOLOGY: This species is named after the former curator at the AMNH, Donn E. Rosen (deceased in 1986), author of many important contributions to biogeography, ich-



Figs. 11–14. *Procolobostema roseni*, n. sp. 11. Female terminalia, ventral view. 12. Same, lateral view. 13. Same, dorsal view. 14. Detail of spinose tergite 10 lobe.

thyology, and phylogeny. He published two classical papers on Caribbean and Mesoamerican biogeography (Rosen, 1976, 1978).

COMMENTS: The female terminalia of *P. roseni*, n. sp., are similar to those of *P. hurdi* Cook, in which both present the typically spinose setae on the distal border of the lobes of tergite 10 (fig. 14). The female tergite 7 of *P. hurdi* has no evident posterior mesal incision, which is obvious in *P. roseni*. The male distal medial notch on sternite 7 of *P. roseni* seems deeper than that of *P. obscurum* (= *P. hurdi*) (if it is a male at all). There is no information on the shape of the male and female sternite 7 of Cook's (1971) species, so they cannot be compared. If the setose structures of the male terminalia of *P. obscurum* (= *P. hurdi*) are the parameres, they are larger in *P. obscurum* than in *P. roseni*, n. sp. Tergite 7 of *P. incisa* is similar to tergite 7 of *P. roseni*, n. sp.

TRIBAL PLACEMENT OF *PROCOLOBOSTEMA*

Cook (1971) stated in his description of *Procolobostema* that the genus is "very like extant *Colobostema* Enderlein in general appearance," and he established similarities and differences between both genera. Cook's (1971) association between *Procolobostema* and *Colobostema* was correct for the systematics of the family at that time. A number of obvious Scatopsinae synapomorphies are present in *Procolobostema*, such as the presence of setae on the front between the antennae and the eye-bridge, and the completely divided epimeron I (Amorim, 1982b). The absence of pediclar setae is a synapomorphy of the Rhegmoclematini also shared by *Procolobostema*. However, 8 flagellomeres and the complete absence of macrotrichia on the posterior veins and membranes of the wing are synapomorphies of the monophyletic group including Scatopsini, Colobostematini, and Swammerdamellini. Moreover, *Procolobostema* possesses the plesiomorphic condition of other characters in the Rhegmoclematini. The presence of a wide scutum, on the other hand, together with the dark coloration of the wing membrane are synapomorphies that indicate the genus belongs to the Colobostematini. The small palpus is a symplesiomorphy, not informative for place-

ment of the genus, but it indicates that the genus does not belong to the Swammerdamellini. The same can be said about the relatively long vein R_5 . Colobostematini, hence, is the best tribal placement for the genus. Other apomorphic features shared by *Procolobostema* and various genera of the tribe reinforce this conclusion.

Colobostematini comprises the Recent genera *Ferneiella*, *Holoplagia*, *Cookella*, *Borneoscatopse*, *Lumpuria*, and *Colobostema* (Amorim, 1994), with the following phylogenetic relationships: (*Ferneiella* (*Holoplagia* (*Cookella* (*Borneoscatopse* (*Lumpuria* + *Colobostema*))))). Cook (1971) described *Procolobostema* prior to his description of *Villoscatopse* (Cook, 1976). More recently, *Villoscatopse* was synonymized by Haenni (1988) with *Lumpuria* Edwards, the latter not considered a valid genus by Cook (1973). *Borneoscatopse* was erected more recently by Freeman (1990), based on a species described by Edwards (1928) from the Oriental Region. Hence, the inclusion of *Lumpuria* and *Borneoscatopse* in the Colobostematini now poses a question on the phylogenetic position of *Procolobostema* not present at the time of Cook's (1971) description of the genus. A list of relevant characters in this discussion follows, with comments on the genera sharing the apomorphic condition. The following list is not intended to exhaust an analysis of the relationships within the tribe, but rather to concentrate on the features that help to place *Procolobostema* in the Colobostematini.

APOMORPHIES AFFECTING THE POSITION OF *PROCOLOBOSTEMA* IN THE COLOBOSTEMATINI

On each transformation series below, the plesiomorphic condition is given first, separated by a bar from the apomorphic state. When more than one apomorphic condition is present, the successive apomorphic conditions are referred to as a, b, etc.

1. *Females holoptic / dichoptic.*
2. *Covering of setae on the compound eyes short / particularly long.*

As far as I am aware, only *Colobostema* has females that reverse the dichoptic condition acquired at the base of Scatopsidae

evolution. The female of *Procolobostema roseni* possesses a slender eye-bridge, but not interrupted as in *Colobostema*. The presence of well-developed interfacetal setae on the eyes is another autapomorphy of *Colobostema*.

3. *Connection of front and face between the antennae absent / present.*

This is an apomorphic feature shared by *Colobostema* and *Lumpuria*. The front is interrupted in all Scatopsidae except in the Aspidinae, which shows the true plesiomorphic condition of the character, also seen in related families. In *Colobostema* and *Lumpuria*, there is an apomorphic, secondary reversion of this feature, connecting the front between the antennae. *Procolobostema* is plesiomorphic for this re-acquisition of the connection.

4. *Single crown of setae on the flagellomeres / large number of setae not organized in crowns on the flagellomeres.*

Typically, the Scatopsidae have a single regular crown of setae on each flagellomere. In *Colobostema* and *Lumpuria* this condition is lost, with macrotrichia scattered irregularly on the flagellomere; in *Lumpuria* the flagellomeres are secondarily elongated. *Procolobostema* has crowns of setae on the flagellomeres.

5. *Suture present between the anepisternum anteriorly and the ventral sclerite of epimeron I / absent.*

A unique feature found in *Colobostema* and *Lumpuria* is the loss of the suture between the anepisternum and the ventral sclerite of epimeron I. Consequently, there is a single, large plate ventrally on the thorax of these two genera anteroventrally. *Borneoscatopse* and *Procolobostema* are certainly plesiomorphic for this character.

6. *Spiracular sclerite (dorsal part of the epimeron I) small / large.*

A large spiracular sclerite—with a central opening—is found in *Borneoscatopse*, *Colobostema*, *Procolobostema* and, to a lesser degree, in *Lumpuria*. A small spiracular sclerite is present in the Scatopsinae ground plan and retained in the Scatopsini, some ba-

sal Rhegmoclematini, *Ferneiella*, *Holoplagia*, and *Cookella*. Some Rhegmoclematini and Swammerdamellini possess a spiracular sclerite elongated anteriorly and posteriorly, a condition different from that found in some Colobostematini genera. The apomorphic condition of this transformation series excludes *Ferneiella*, *Holoplagia*, and *Cookella* from a monophyletic group including *Borneoscatopse*, *Colobostema*, *Procolobostema*, and *Lumpuria*.

7. *Anterior katepisternal setae present / absent.*

Anterior katepisternal setae in the Colobostematini are absent only in *Colobostema* and *Lumpuria*. There are some genera of other tribes that are also apomorphic for this character, but I consider this a homoplastic development.

8. *Meral setae.*

The presence of meral setae is apparently an autapomorphy of *Borneoscatopse* inside the Colobostematini.

9. *Anepisternum with pubescence restricted to the dorso-posterior half / anepisternum entirely covered with microtrichia.*

The presence of an entirely pruinose anepisternum is an apomorphy shared by *Colobostema*, *Lumpuria*, *Borneoscatopse*, and *Procolobostema*. This is not a unique condition in the family, but is apomorphic within the tribe. This feature has the same distribution as character 6, reinforcing the monophyly of the group.

10. *Scutum elongated / scutum short, about as wide as long.*

The relatively wide scutum which is elongated at the family ground plan is an apomorphic feature that originated twice in the Scatopsidae: in *Parascatopse* (a Rhegmoclematini genus of minute specimens), and in all Colobostematini except *Ferneiella*. In *Colobostema*, *Lumpuria*, *Borneoscatopse*, and *Procolobostema* the thorax is particularly well developed.

11. *Pedicelar setae present / absent.*

This character is apomorphic in the Rhegmoclematini and in *Lumpuria*. This led Cook

(1976) to consider the possibility that *Villoscatopse* (= *Lumpuria*) is related to the Rhegmoclematini. However, there are few doubts that this is a homoplastic appearance of the character in the two tribes.

12. *Supra-alar setae present / supra-alar setae scarcely differentiated or absent.*

The loss of differentiated supra-alar setae is a synapomorphy uniting *Lumpuria* and *Colobostema*. It is also known to be apomorphic in the Rhegmoclematini genus *Parascatopse*.

13. *CuA₂ gradually approaching margin after a basal curve / curved posteriorly near margin.*

Holoplagia, *Cookella*, *Borneoscatopse*, and *Procolobostema* have CuA₂ curved continuously, reaching the wing margin in a proximal position. In *Ferneiella*, *Colobostema*, and *Lumpuria*, on the other hand, a second curve turns the distal third of CuA₂ to a distal position on the wing. The condition found in *Ferneiella* is quite like that of the Scatopsini, so it can be viewed as truly plesiomorphic. It is most parsimonious for the shape of the vein in *Holoplagia*, *Cookella*, *Borneoscatopse*, and *Procolobostema* to be a synapomorphy of all Colobostematini (except *Ferneiella*), then reversed at the base of the (*Colobostema* + *Lumpuria*) clade.

14. *Secondary r-m vein present / a. partially present / b. absent in males.*

Amorim (1982b) proposed that the spurious r-m crossvein is probably a synapomorphy of the Scatopsini⁺ (Scatopsinae except Rhegmoclematini), with secondary reductions in some of its subgroups. A partially or completely developed r-m is known in the Scatopsini (*Scatopse* and *Pharsoreichertella*), Colobostematini, and Swammerdamellini (*Pararhexosa*). Within the Colobostematini the secondary R₅-M₁ crossvein is complete in *Cookella*, most *Holoplagia*, and some *Colobostema*; incomplete in *Ferneiella*, *Lumpuria*, and most *Colobostema*. In *Borneoscatopse* it is clearly absent, while in *Procolobostema* it is absent in most males, but clearly present and incomplete in most females. It is difficult to determine how the feature evolved in the tribe. Beginning with a com-

plete vein in the tribal ground plan, it seems most parsimonious to admit three independent events of interruption of the vein: in *Ferneiella*, within *Holoplagia* (not appearing at the cladogram in fig. 15), and at the ground plan of the group (*Borneoscatopse* + *Procolobostema* + *Lumpuria* + *Colobostema*) a complete loss would be homoplastic between *Ferneiella* and the males of *Borneoscatopse* and *Procolobostema*.

15. *Base of M₁ complete in males / males with base of M₁ interrupted.*

An incomplete base of M₁ in the Scatopsidae is not uncommon, seen in the Aspistinae, Psectrosciarinae, and some Rhegmoclematini. Within the Colobostematini, a basally interrupted M₁ is seen only in *Borneoscatopse* and in the males of *P. roseni*. It is not clear whether the (supposedly) male specimens of *Procolobostema* described by Cook (1971) are apomorphic for the feature. The female holotype of *P. hurdi* has a wing similar to that of *P. roseni*, with a basal angle at M₁ with a suggestion of R₅-M₁. There is no wing drawing for *P. obscurum*, but it is said to have "venation identical to *P. hurdi*." The drawing of the wing of the "female" holotype of *P. incisa* (possibly a male) shows an apparent basal interruption of M₁. Even though the female of *B. curvata* is not known, this feature is accepted here as a synapomorphy for (*Borneoscatopse* + *Procolobostema*).

16. *Posterior veins reaching wing margin / CuA₂ distally incomplete.*

Ferneiella, *Colobostema*, and *Lumpuria* show the apomorphic condition of this transformation series. Outgroups have the plesiomorphic condition. The condition in *Ferneiella* is homoplasious in relation to that of *Colobostema* and *Lumpuria*.

17. *Posterior veins reaching wing margin / CuA₁ incomplete.*

Lumpuria and *Colobostema* have not only CuA₂ but also CuA₁ distally incomplete, a condition not shared by *Ferneiella*.

18. *Tarsi brown / tarsi yellowish.*

The apomorphic condition of this feature

is shared by all Colobostematini except *Ferneiella*.

19. *Gonostyles short / gonostyles elongated.*

Gonostyles are rather short in *Borneoscatopse*, as in the Colobostematini ground plan. Elongated gonostyles is an apomorphy shared by *P. roseni* and, as much as it can be inferred from the original description, *P. hurdi*.

20. *Parameres present / absent.*

Cookella and *Borneoscatopse* do not present parameres in the male terminalia. This condition is apparently also present in *Procolobostema*. I consider the origin of this character to be homoplasious between *Cookella* and (*Borneoscatopse* + *Procolobostema*).

21. *Aedeagus short / a. elongated / b. very elongated.*

22. *Male terminalia short / elongated.*

23. *Male terminalia symmetrical / a. slightly asymmetrical / b. strongly asymmetrical.*

24. *Male cerci present / lost.*

Ferneiella and *Holoplaga*, in the Colobostematini, show the short, plesiomorphic condition for the length of the aedeagus. All remaining members of the tribe have an aedeagus at least slightly elongated, which is probably a synapomorphy of this group. In *Lumpuria* and *Borneoscatopse* the aedeagus is very elongated, possibly a condition derived independently. The terminalia are elongated in *Lumpuria* and in *Cookella* (another homoplasy). On the other hand, a certain degree of asymmetry, certainly an apomorphic condition, is observed in *Lumpuria*, *Colobostema*, and is particularly pronounced in *Borneoscatopse*. *Procolobostema* appears to have a degree of asymmetry similar to that in *Colobostema*. Finally, the absence of cerci is an apomorphy shared by all Colobostematini except *Ferneiella*.

25. *Female lobes of tergite 10 with normal setae along its posterior margin / with spinose setae.*

Spinelike setae along the distal margin of female tergite X of *P. roseni*, n. sp., and *P. hurdi* Cook are obviously apomorphic. This condition is not known in any other scatopsid

group. The only species of *Borneoscatopse*—*P. curvata* (Edwards)—is known only from a male, so it is not possible to determine the condition of the genus for that character. It is accepted provisionally as a synapomorphy of *Procolobostema*.

COLOBOSTEMATINI CLADOGRAM TOPOLOGY
(fig. 15)

The discussion above reveals that *Lumpuria* and *Colobostema* are probably sister groups among the Colobostematini. *Ferneiella* probably is the sister group of the remaining members of the tribe, and *Lumpuria*, *Colobostema*, *Borneoscatopse*, and *Procolobostema* seem to form a monophyletic group. Many similarities between *Procolobostema* and *Borneoscatopse* are actually plesiomorphic features in the group (*Lumpuria* + *Colobostema*). However, the shape of M_1 as well as the loss of parameres would be synapomorphic for the apparent clade (*Procolobostema* + *Borneoscatopse*). Even though more evidence is certainly desirable to confirm that *Borneoscatopse* and *Procolobostema* are sister groups within the Colobostematini, this seems the more parsimonious interpretation with the available data. *Borneoscatopse curvata* is a species quite aberrant for the wing and male terminalia, which makes comparisons with other species quite difficult. If new species related to *B. curvata* are described, relationships of the two genera may be clarified.

COLOBOSTEMATINI CLASSIFICATION

The classification presented below updates that presented by Amorim (1994), in which *Procolobostema* did not appear. There are not sufficient Linnaean categories between tribe and genus to name all levels in the cladogram; therefore, a partially sequenced phylogenetic classification is erected (see Nelson, 1972, 1973), also using the group⁺ artifact (Amorim, 1982a) to refer to unnamed inclusive taxa in the classification. Square brackets are used for redundant names of monotypic taxa.

Colobostematini

Ferneiella Cook in Freeman, 1985
Holoplaga Enderlein, 1912

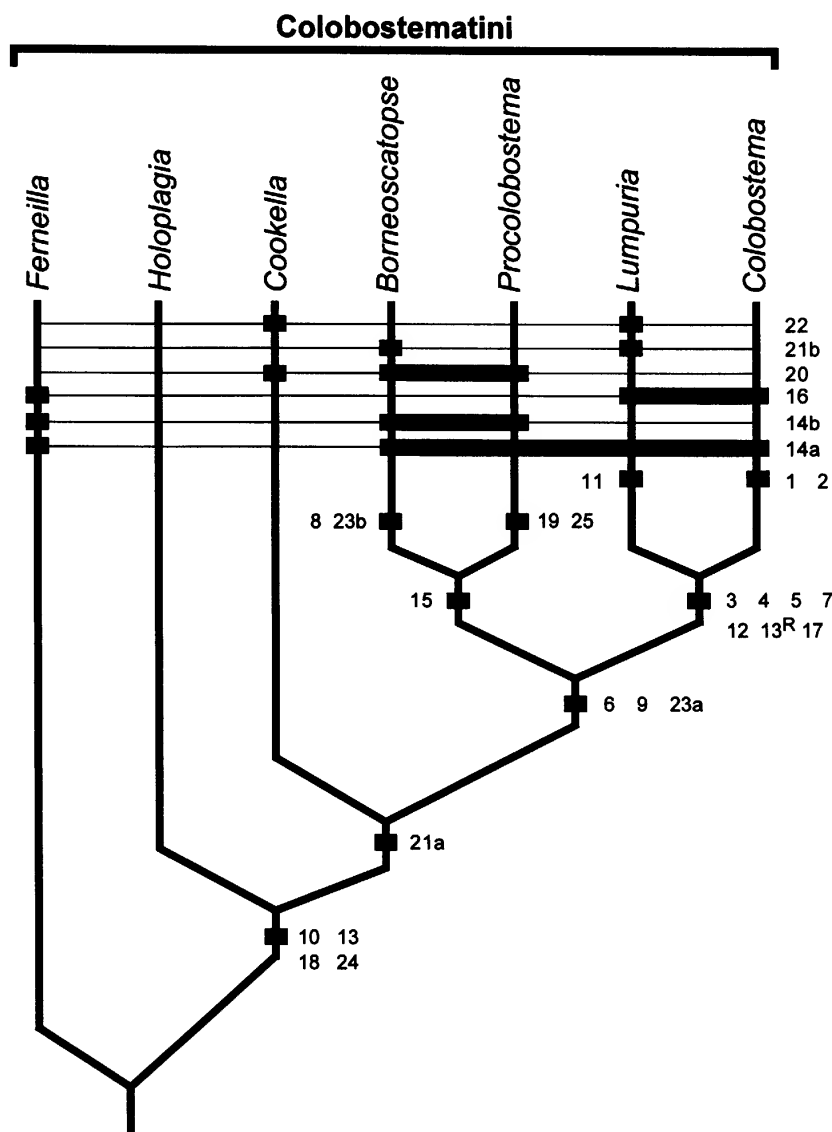


Fig. 15. Cladogram for the phylogenetic relationships within the Colobostematini. See text for list of transformation series. Homoplasies are placed on the top of the cladogram; features of unique origin within the group appear at the joining stems.

Cookella Freeman, 1985

group *Procolobostema*⁺

Procolobostema Cook, 1971

Borneoscatopse Freeman, 1990 [*B. curvata* (Edwards, 1928)]

Lumpuria Edwards, 1928

Colobostema Enderlein, 1926

HISTORICAL INFERENCES

The relationships hypothesized between *Borneoscatopse* and *Procolobostema* present

some interesting biogeographical implications. *Borneoscatopse curvata* (Edwards), from Borneo, would be the only Recent representative of a taxon apparently much more widely distributed in earlier times, preserved in mid-Tertiary amber from Dominican Republic (Hispaniola) and Chiapas (Mexico). *Colobostema* is a cosmopolitan group. Different scatopsid groups present a clear Laurasia × Gondwanaland pattern of division that groups *scatopsiformis* of *Psectrosiara*

(Amorim and Haenni, 1992), the Rhegmoclematina, *Quateiella*, and *Abrhexoza*. Also, *Colobostema* itself presents a similar division (Amorim, 1982b) so it does not seem to be untenable to admit that the genus has a Pangaeian origin. Since *Lumpuria* is its sister group, it would have the same age as *Colobostema*; the origin of the *Procolobostema*⁺ clade, one level below in the cladogram, would be necessarily still older than that and, hence, should have been already differentiated in Pangaea.

A Pangaeian origin for a taxon implies differentiation prior to the beginning of the Jurassic. As discussed above, the Upper Jurassic fossil species *Protoscatopse jurassica* Rohdendorf has features of Recent scatopsid groups. The presence of a number of Eocene to Miocene amber species clearly belonging to Recent genera also does not contradict such a hypothesis. Biogeographical distribution of some subgroups of the family, on the other hand, is congruent with the separation of Laurasia and Gondwanaland (see Amorim and Haenni, 1992). Hence, both from a biogeographical and a paleontological point of view, a Pangaeian origin for some taxa of generic rank in the Scatopsidae is not an unlikely hypothesis.

If this theory is correct, the biogeographical distribution of the (*Borneoscatopse* + *Procolobostema*) clade, on the other hand, is not particularly congruent with a Northern/Southern Hemisphere pattern (congruent with the Laurasia/Gondwanaland division), which is more common for intercontinental relationships. The pattern seen in this clade, however, is not completely bizarre. Other groups present such Southeast Asia–Australia/Caribbean disjunction. Two of the most famous are that of *Mastoterme*s (in Mexican

and Dominican amber and with one living species in Australia) and the *Leptomyrme*s ants (in Dominican amber, with living species in New Caledonia, New Guinea, and Australia). Another case is that of *Valeseguya* Colless (Diptera: Anisopodidae), known from a single Australian Recent species (Colless, 1990) and an extinct species described from a large series in Dominican Republic amber (Grimaldi, 1991). The disjunction between the drosophilid genera *Mayagueza*, in Puerto Rico, and *Acletoxenus*, in the Oriental Region, described by Grimaldi (1988), is also congruent with this pattern. These and other cases may actually point to a general biogeographical component related to the hypothetical Pacifica continent (Howell et al., 1984), originally suggested by Croizat's (1958) biogeographical studies, and in more detail by Nelson (1985).

It is noteworthy that in the lower Miocene the Proto-Antilles and nuclear Central America were already fragmented (Rosen, 1976), so Mexico and Hispaniola were already separated (Pindell and Dewey, 1982; Burke, 1988; Ross and Scotese, 1988). Fossil species of *Procolobostema* in Mexico and Hispaniola indicate that the ancestral species of the genus occupied at least the whole Proto-Antilles arch and nuclear Central America. Quite clearly, different extinction events eliminated the Dominican and Mexican species of *Procolobostema*. There is no indication as to when—between the Miocene and Recent—these extinction events precisely took place. The obvious possibility would be to attribute the extinctions to climate fluctuations in the Miocene, but this raises the question as to why other genera (such as *Ectateta* and *Neorhegmoclemina*) preserved in the Dominican and Mexican ambers remained intact to the present.

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